EVOLUTIONARY RESPONSES OF MARINE INVERTEBRATES TO INSULAR ISOLATION IN GALAPAGOS

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SUMMARY

I examine the natural barriers to distribution and colonization that have shaped the Galapagos marine invertebrate biota. While diversity is high for some groups, such as hydroids and bryozoans, it is low for many others. Porcelain crabs and molluscs are examples with reduced or unbalanced representation in Galapagos, resulting from their dependency on dispersal of relatively short-lived planktonic larvae by ocean currents and on habitat limitations in Galapagos. Because Galapagos shorelines are predominantly rocky, without the wide expanses of silt typical of much of the Ecuadorian mainland that are favored by infaunal bivalves, gastropod diversity in Galapagos far exceeds that of bivalves. Nearly all hermatypic corals in Galapagos are members of the Panamic province; none is endemic to Galapagos. This suggests that colonization occurred by larval dispersal from there. The ahermatypic (azooxanthellate) coral fauna of Galapagos, with 43 species, is richer and more diverse than the hermatypic corals, with 29% of the shallow-water ahermatypes endemic and the remainder with Panamic, Indo-Pacific, and cosmopolitan affinities. The 73 verified species of Galapagos shallow-water echinoderms are dominated by Panamic species, with additional affinities to the Indo-Pacific and the California province; 8% are cosmopolitan and 8% endemic. With species richness roughly equivalent to that of Pacific Colombia, Galapagos echinoderm representation is not depauperate, but is sufficiently distinctive to characterize it as an isolated, insular biota. Hydroids and bryozoans, two groups with high diversity in Galapagos, accomplish long-distance transport mainly as adults on floating debris and hulls of ships, rather than by the free-swimming reproductive stage. Endemism among marine invertebrates averages 18.3 %, but varies widely among major taxa, from 0% for reef corals to 71% for gorgonians. Unlike the Galapagos terrestrial biota, in which endemic genera are common, the absence of endemic genera among marine invertebrates may be attributed to low isolation arising from greater dispersal and gene flow in the marine environment.

RESUMEN

Respuestas evolutivas al aislamiento insular de los invertebrados marinos en Galápagos. En este reporte examino las barreras naturales para la distribución y colonización que han modelado la biota de los invertebrados marinos de Galápagos. Mientras la diversidad es alta en algunos grupos, tales como hidroides y briozoos, es baja en muchos otros. Los cangrejos porcelana y moluscos son ejemplos con representación reducida o no balanceada en Galápagos, resultante de su dependencia en la dispersión por corrientes oceánicas de su larva planctónica de relativamente corta vida, y de limitaciones de hábitat en Galápagos. Debido a que las costas de Galápagos son predominantemente rocosas, sin las amplias extensiones de limo típicas de muchas de las costas ecuatorianas que son favorecidas por la infauna de bivalvos, la diversidad de gasterópodos en Galápagos excede por mucho la de los bivalvos. Casi todos los corales hermatípicos en Galápagos son miembros de la provincia Panámica; ninguno es endémico para Galápagos. Esto sugiere que la colonización ha ocurrido por dispersión larval desde dicha provincia. La fauna de corales ahermatípicos (azooxantelados) de Galápagos, con 43 especies, es más rica y más diversa que en los corales hermatípicos, con un 29% de especies de poca profundidad endémicas y las otras con afinidades Panámicas, Indopacíficos y cosmopolitas. Las 73 especies de equinodermos de poca profundidad verificadas para Galápagos están dominadas por especies Panámicas, con afinidades adicionales para el Indopacífico y la provincia de California; 8% son cosmopolitas y 8% endémicas. Con una riqueza de especies aproximadamente equivalente a la del Pacífico colombiano, la representación de los equinodermos de Galápagos no está depauperada, pero es lo suficientemente distintiva como para caracterizarla como una biota insular aislada. Hidroides y briozoos, dos grupos con alta diversidad en Galápagos, logran ser transportados largas distancias, principalmente como adultos sobre restos flotantes y cascos de barcos, más que por el estado reproductivo de libres nadadores. El promedio de endemismo entre invertebrados marinos es de 18.3%, pero varia ampliamente entre las principales taxas, desde el 0 % para corales hermatípicos hasta 71% para gorgonias. En contraste a la biota terrestre de Galápagos, la cual cuenta con muchos géneros endémicos, la ausencia de géneros endémicos entre los invertebrados marinos puede ser atribuida al bajo aislamiento que resulta de la mayor dispersión y flujo genético en los ambientes marinos.

INTRODUCTION

It has long been recognized that the flora and fauna of the Galapagos terrestrial environment are unbalanced compared to South American mainland biota. While some animal groups, such as reptiles, seabirds, marine mammals and land snails are well represented, others, such as amphibians, song birds, land mammals, aquatic insects, and freshwater fish are poorly represented or absent (Jackson 1993). Groups with obvious adaptations for dispersing long distances tend to be disproportionately common. Is this disharmonic representation also present in the marine environment of Galapagos? Answering this is hampered by uneven taxonomic investigations in the marine environment of the equatorial east Pacific, where some invertebrate groups have received much more attention than others. Before the introduction of scuba diving in the 1950s, explorations of subtidal life depended mainly on dredging, a notoriously clumsy and non-selective way to collect marine invertebrates. Nevertheless, the extensive collections of earlier expeditions, together with more recent surveys, allow us to begin to compare the marine biota of Galapagos with that of the South American mainland coast.

Diversity is high for groups with good dispersal, such as hydroids (Calder *et al* 2003), bryozoans (Banta 1991), cirripedians (Zullo 1991) and caridean shrimps (Wicksten 1991, Wicksten & Hendrickx 2003), but considered low for many other groups, such as molluscs (Finet 1991, 1994), echinoderms (Maluf 1991), benthic polychaetes (Blake 1991), hermatypic corals (Glynn 2003), and porcelain crabs (Haig 1960, Harvey 1991). Table 1 summarizes the number of species and degree of endemism in Galapagos marine groups. The proportion of both shore-dwelling and deep-water endemic marine organisms totals about 18%; this is comparable to other oceanic islands and archipelagoes, which range from 0 to 20% (Bustamante *et al.* 2002).

Trans-oceanic dispersal is heavily influenced by oceanic currents and the distribution of islands that may act as stepping stones. The Galapagos archipelago lies at the confluence of three oceanic currents (Fig. 1). The main current is the South Equatorial Current (SEC) which is fed principally by the cool (20–24°C) Peru Oceanic Current (POC). The Peru Coastal Current (PCC) carries cold water (as low as 13°C) but is separated from the POC by the Peru Coastal Countercurrent. When the POC reaches Galapagos its temperature is 18–22°C. The SEC is supported throughout the year by southeasterly trade winds that vary in strength seasonally. It is a strong current during much of the year, traveling 80–160 km per day. The Equatorial Undercurrent upwells along the western wall of the Galapagos Platform, bringing cold water (14–16°C) to the western islands. It is also nutrient rich, producing great productivity in this area. The Panama Current, a composite of the California Current and the North Equatorial Countercurrent, is a slow-moving current bringing to Galapagos warm water (26–29°C), low in salinity and low in nutrients, usually in January when the southeasterly trade winds slacken (Banks 2002, Chavez & Brusca 1991, Wyrtki 1985). During El Niño years, this current is believed to transport Panamic species to the Galapagos. A consequence of this complex current system is marked variation in oceanographic conditions across the archipelago. During El Niño years, regional variation in conditions disappears as water temperatures rise above 25°C.

Oceanic currents make possible the dispersal of species between widely separated areas, especially species capable of long-distance larval transport. Currents also serve as barriers to dispersal. The principal barriers to east–west distribution are the Central American land barrier to the east and the E Pacific Barrier to the west (Fig. 2). The

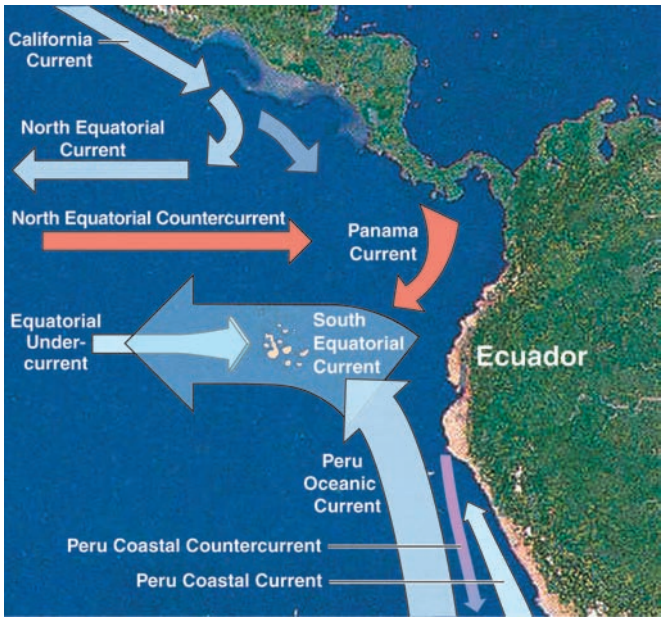

Figure 1. Currents of the east Pacific.

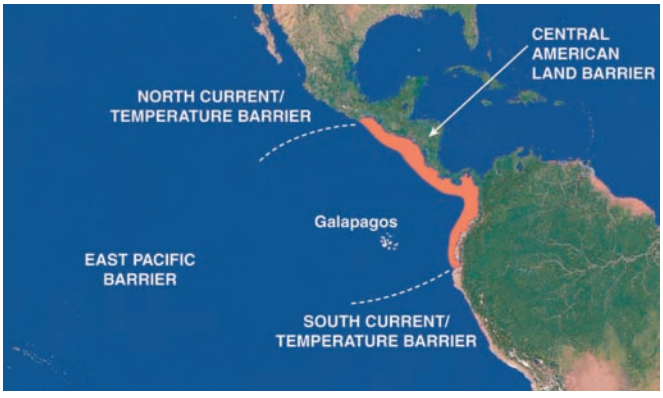

Figure 2. Barriers to larval dispersal in the Pacific.

latter, often referred to as Ekman's East Pacific Barrier (Ekman 1953), is an enormous expanse of water between the Indo-Pacific and east Pacific, presenting virtually no opportunity for island hopping. The Line Islands, the central Pacific islands closest to Galapagos, are more than 7500 km away. The major eastward-flowing current is the North Equatorial Countercurrent (NEC) with a mean flow of about 35 km/day (Wyrtki & Kilonsky 1984), although highly variable seasonally.

PORCELAIN CRABS

The porcelain crabs (Decapoda: Anomura: Porcellanidae) provide insights into the origins of Galapagos marine invertebrates. Because they are among the most abundant crustaceans in sheltered cobble or boulder coastal habitats, porcelain crabs have been considered ideal for studies of congeneric physiological adaptation and distribution (Villalobos Hiriart *et al.* 1992, Stillman 2002). Despite their resemblance to brachyurans, they are anomuran decapods with huge claws in relation to body size and three pairs of usable walking legs, the fourth pair much reduced and folded forward over the abdomen. They feed by trapping plankton on highly setose mouth appendages which they wave through the water (Fig. 3). They are common in the intertidal and shallow subtidal zones of Galapagos, clinging to the underside of stones or associated with corals or sponges. The 14 recognized species, eight of which are considered common in Galapagos (Hendrickx & Harvey 1999, Hickman & Zimmerman 2000), are a homogeneous group: all are filter feeders, with similar ecology and morphology. Three of the 14 are endemic to Galapagos (Table 1).

Figure 3. Porcelain crab *Pachycheles biocellatus,* showing the setose mouth appendages used in feeding.

Of the *c.* 250 known species of porcelain crabs worldwide, approximately 180 occur in the Pacific (Table 2). Of these, about 90 species are in the Indo-Pacific and 92 in the east Pacific with no overlap between the two regions (Haig 1960, Harvey 1991, Hiller *et al*. 2004). The affinity of

Table 1. Number of marine species in major taxonomic groups of Galapagos, after Bustamante *et al*. (2002), expanded and updated to include additional groups.

Group	No. of species	No. of endemics	Percent endemic	Species richness	Level of study
Mammals	24	2	8.3	High	Good
Marine birds	19	5	26.3	High	Good
Fishes	447	51	11.4	Intermediate	Moderate
Polychaetes	192	50	26	Intermediate	Poor
Amphipods	50	19	38	Intermediate	Good
Brachyurans	120	23	19.2	Intermediate	Poor
Caridea & Stenopods	65	10	15.4	High	Poor
Porcelain crabs	14	3	21.5	Low	Moderate
Barnacles	18	4	22.2	Low	Moderate
Molluscs	780	141	18.1	Low	Moderate
Opisthobranchs	49	18	36.7	Low	Poor
Echinoderms	200	34	17.0	Low	Moderate
Bryozoans	184	34	18.5	High	Poor
Sea anemones	15	2	13.3	Low	Poor
Zoanthids	7	?	?	Low	Poor
Gorgonians	14	10	71.4	Intermediate	Poor
Sea pens	4	2	50	Low	Poor
Cerianthids	2	0	0	Low	Poor
Hydroids	96	14	14.5	High	Moderate
Corals, hermatypic	23	0	0	Low	Good
Corals, ahermatypic	43	17	39.5	Intermediate	Poor
Algae	333	130	39	High	Poor
Soft bottom meiofauna communities	390	?	?	High	Poor
Overall	**3089**	**569**	**18.3**		

Table 2. Comparing Galapagos porcellanids to other regions. Adapted from Harvey (1991).

Region	No. of species	Shared species
Pacific total	180	14
Indo-West Pacific	90	0
Eastern Pacific	92	14
Alaskan–Oregonian	4	0
Californian	26	0
Cortez–Mexican	41	7
Panamanian	61	13
Peruvian–Chilean	14	1

the 11 non-endemic Galapagos porcellanids is overwhelmingly with the Panamic province, which extends from the Gulf of Tehuantepec (southern Mexico) to the Gulf of Guayaquil (southern Ecuador) or Paita in northern Peru (Briggs 1974) (Fig. 4). Seven of these 11 are shared with the Cortez–Mexican province and one is shared with the Peruvian province. None of them occurs north of the Cortez–Mexican province.

Of the 92 species of porcellanids in the east Pacific, 32 occur in Ecuador and 41 in Pacific Colombia (Table 3). If we accept these as the major source pool for the Galapagos fauna, with a combined 42 species, we can ask why only

Figure 4. Marine provinces of the east Pacific.

Table 3. Representation of Panamic genera of porcelain crabs in Galapagos, Ecuador and Colombia.

Genus	Galapagos[1]	Ecuador[2]	Colombia[3]	Panama[4]
Petrolisthes	8[5]	15	19	20
Pachycheles	2	7	7	8
Neopisosoma	2	2	3	2
Clastotoechus	1	1	2	1
Polyonyx	1	1	1	1
Megalobrachium	0	2	4	5
Euceramus	0	1	0	2
Porcellana	0	1	2	3
Pisidia	0	1	1	1
Ortochela	0	1	1	1
Minyocerus	0	0	1	0
Ulloaia	0	0	0	1
Totals	14	32	41	45

[1]From Haig (1960), Hickman (2000)
[2]From Haig (1960), Hiller *et al.* (2004)
[3]From Hiller *et al.*(2004), Lazarus-Agudelo (2006)
[4]From Gore & Abele (1976)
[5]Added in proof. A ninth species, *Petrolisthes donadio* Hiller and Werding 2007, was discovered among my specimens after completion of this manuscript.

14 species occur in Galapagos. Harvey (1991) describes two principal elements that could have contributed. One is the short dispersal phase during larval development; compared to other decapod crustaceans, porcellanids produce few large eggs with accelerated larval development and are thus poorly suited for long-distance oceanic transport. Second, dispersal of porcellanid larvae, like any planktonic larvae, is wholly dependent on the pattern of oceanic currents. Porcellanid larvae hatched in the central Pacific would have to be transported at least at 10 times the rate of the NEC to reach Galapagos or any other islands in the east Pacific (Harvey 1991). For porcelain crabs, the East Pacific Barrier is complete: no Indo-Pacific porcellanids have established populations in the east Pacific and no east Pacific porcellanids are known to have successfully established populations in the Indo-Pacific.

Additional barriers are the north and south current-temperature barriers (Fig. 2). From California southwards, the current is unfavorable most of the year and the water too cold for tropical porcelain crabs. From the south, the only Galapagos porcelain crab with Peruvian affinity, *Petrolisthes armatus*, is known from a single record and considered "extralimital" by Haig (1960). It has not appeared in recent collections. A possible explanation for the absence of porcellanids of Peruvian affinity is that the POC, which gives rise to the SEC that flows directly through Galapagos, is separated from the PCC by the Peru Coastal Countercurrent (Fig. 1), which acts as a barrier to larval dispersal northward from coastal Peru (Fig. 2). Also, because the continental shelf along Peru is narrow and strong currents sweep offshore, pelagic larvae would be swept out to sea beyond a site for safe

settlement. Consequently there has been selection for more direct development with fewer, larger eggs, and for reduction or complete omission of prolonged, free-swimming larval stages that might be distributed as far as Galapagos.

Ten of the 14 Galapagan porcelain crabs are of just two genera (Table 3), *Petrolisthes* and *Pachycheles*, which are the most specious, both within the Panamic province and worldwide (Harvey 1991, Stillman & Reeb 2001), suggesting that the porcelain crabs of Galapagos have passed through a dispersal filter that allowed only species with good dispersal and colonizing ability to become established there. Additionally, habitat diversity is limited in Galapagos as compared to coastal mainland Ecuador and Colombia. For example, Bahía Málaga in Pacific Colombia, with 32 species of porcellanids, has high coastal habitat diversity with extensive mangroves, mudflats, intertidal rocky shores and depositional sand beaches (Lazarus-Agudelo & Cantera-Kintz 2007). Galapagos shorelines, consisting mainly of sloping rocky lava fields with interspersed sand and gravel pockets and occasional shoreline mangroves, offer more limited habitat resources for porcellanids, for which the Galapagos can be considered a diminutive outpost of the Panamic province, the apparent exclusive source of its porcellanid fauna.

MOLLUSCS

The marine molluscs of Galapagos have been thoroughly sampled and described, the result of several expeditions over the past century, as well as extensive collecting by the De Roy and Angermeyer families of Puerto Ayora. There are *c.* 780 shallow-water marine molluscs in Galapagos (Kaiser 1997), as compared with *c.* 1200 in continental Ecuador, based on recent surveys by the Nazca Institute for Marine Research (K. Clark, pers. comm.) and more than 3000 species in the Panamic Province (Keen 1971).

Molluscs of the Panamic province exhibit the greatest diversity of all east Pacific provinces (Roy *et al*. 1994) but distributional patterns differ significantly between the northern and southern reaches of the province. Dispersal is by pelagic larvae and, unlike the porcelain crabs, many gastropod groups have teleplanic larvae with sufficiently long pelagic life to cross the East Pacific Barrier (Finet 1991). Some adults may cross this barrier on floating debris, especially during El Niño years when, for example, the grapsoid crab *Plagusia immaculata* and the swimming crab *Euphylax dovii*, the latter often in enormous numbers, appear in Galapagos (Hickman & Zimmerman 2000).

Table 4. Zoogeographical affinities of the marine molluscs in Galapagos (from Finet 1991).

Affinity	No.	%
Endemic	125	21
Pure Panamic	337	57
Panamic + Californian	46	8
Pure Californiana	0	0
Panamic + Peruvian	42	7
Pure Peruvian	3	0.5
Panamic + Caribbean	10	1.7
Pure Indo-Pacific	13	2
Circumtropical	14	2.2

Table 5. Numbers of species and percentage of the respective total marine molluscan fauna in Galapagos and continental Ecuador.

	Galapagos[1]		Ecuador[2]	
Class	Number	%	Number	%
Cephalopoda	8	<1	6	<1
Scaphopoda	8	<1	6	<1
Bivalvia	201	26	347	39
Gastropoda	537	70	527	59
Polyplacophora	13	2	5	<1

[1]From Kaiser, 1997
[2]Numbers are minimal, representing incomplete analysis of collections (K. Clark pers. comm.).

Some 13 species of Galapagos molluscs have pure Indo-Pacific affinities (Table 4). For north–south distribution, mollusc dispersal is limited by the same thermal-current barriers that operate against the porcellanids. No Galapagos molluscs have pure Californian affinity and only three have pure Peruvian affinities. However, some 46 Galapagos species have a Panamic–Californian distribution. As Finet (1991) suggests, these are probably Panamic species that have been carried north when coastal currents flow northward during the northern summer.

Compared to the mainland, Galapagos is rich in gastropods and relatively poor in bivalves (Table 5). On the Ecuadorian coast, the ratio of gastropods to bivalves is approximately 1.5:1 (K. Clark pers. comm.), while in Galapagos it approaches 3:1 (Table 5). There also has been clear selection against bivalves that burrow or live in sand compared to those living on top of, or attached to, the benthos: on the mainland coast there are nearly four times as many infaunal bivalves as epifaunal, whereas in Galapagos these are approximately equal in number (Kay 1991). A principal reason for the prominence of gastropods is that Galapagos shores are rocky, dropping away quickly to deep water. There is a scarcity of the wide expanses of silty, sandy ocean bottom, typical of the mainland coast (Fig. 5), that are required to support large numbers of infaunal bivalves.

Approximately 18% (141 of 780 species) of the Galapagos shallow-water molluscs are considered endemic (Finet 1991) and most of these are gastropods. Endemism is strictly at the species level. Establishing endemism is not a simple matter. Species thought to be endemic to their region of occurrence are later frequently found elsewhere. The percentage of endemism for Galapagos molluscs will doubtless decline as coastal field studies now underway in Ecuador and Colombia bring results. Future molecular

genetic studies also may reveal some presumed endemics to be east Pacific species obscured by phenotypic differences between island and mainland populations.

SCLERACTINIAN CORALS

The reef-building (hermatypic or zooxanthellate) coral fauna of the equatorial east Pacific is impoverished and patchy in distribution compared to the central and west Pacific, with a pronounced pattern of increasing species richness from east to west (Veron 1995). From the equatorial east Pacific with 32 species (excluding the *Millepora* hydrocorals) diversity increases just west of the East Pacific Barrier to approximately 100 species in the central Pacific. Species richness increases steadily to 450 species in the Philippine and north Indonesian archipelagoes. More than 500 west and central Pacific hermatypic coral species have been described (Veron 2000).

The reef-building corals of Galapagos, while locally abundant in the north, are restricted by limited shallow-water habitat required for reef development, by an abundance of bio-eroding organisms and, especially, by periodic El Niño events. In recent years, Galapagos reefs were almost entirely destroyed by the 1982–3 and 1997–8 El Niño events. Recovery has been slow and several species that were once abundant are now uncommon (Glynn 2003). None has become extinct, however. Galapagos, with 22 species of reef-building corals, shares with the Panamic province a coral fauna dominated by two genera: *Pocillopora* (9 species) and *Pavona* (5 species) (Table 6). The remaining seven species, belonging to six genera, are uncommon, with the exception of *Porites lobata*, a resilient reef-building species that has rapidly recovered from the 1982–3 and 1997–8 El Niño events to become the dominant coral in Darwin and Wolf. Despite periodic El Niño disturbances, Galapagos supports as many coral species as Ecuador and Colombia and only slightly fewer than Panama (22 in Galapagos, 26 in Panama), the latter considered a more favorable coral habitat. For hermatypic corals, Galapagos is a remarkable exception to the effect of island impoverishment compared to mainland source areas.

The origin of the coral reef fauna of the east Pacific has been a matter of controversy (Glynn & Wellington 1983, Veron 1995, Glynn & Ault 2000). A long-distance dispersal hypothesis (Dana 1975) holds that the east Pacific corals are comparatively recent immigrants, by long-distance larval transport and recolonization from the central Pacific following massive extinction of east Pacific corals

Figure 5. A sand-silt beach of mainland Ecuador, important habitat for infaunal molluscs.

Table 6. Presence/absence of hermatypic corals of the equatorial east Pacific in Galapagos (G), mainland Ecuador (E), Colombia (C), Panama (P), central Pacific (CP) and Indo-Pacific (IP). + = present; – = not recorded

E Pacific species that occur in:	G[1]	E[2]	C[3]	P[4]	CP[5]	IP[6]
Pocillopora damicornis	+	+	+	+	+	+
Pocillopora verrucosa[7]	+	+	+	+	–	+
Pocillopora elegans[7]	+	+	+	+	+	+
Pocillopora eydouxi	+	+	+	+	+	+
Pocillopora ligulata	+	–	–	+[8]	+	–
Pocillopora meandrina	+	–	–	+	+	+
Pocillopora capitata	+	+	+	+	–	+
Pocillopora inflata	+	–	–	+	–	–
Pocillopora woodjonesi	+	–	–	–	+	+
Pocillopora effusus	+	+[8]	–	–	–	–
Pocillopora danai	–	–	+	–	?	+
Acropora valida	–	–	+	–	+	+
Porites lobata	+	+	+	+	+	+
Porites panamensis	–	+	+	+	–	–
Psammocora stellata	+	+	+	+	+	+
Psammocora superficialis	+	+	+	+	+	+
Psammocora brighami	–	+	–	+	––	–
Psammocora obtusangula	–	–	+	+	+	+
Gardineroseris planulata	+	+	+	+	+	+
Siderastrea glynni	–	–	–	+	––	–
Leptoseris scabra	+	–	–	–	+	+
Leptoseris papyracea	–	+	+	+	+	+
Leptoseris foliosa	–	+	––	–	–	+
Pavona clavus	+	+	+	+	+	+
Pavona frondifera	–	–	+[8]	+	–	+
Pavona gigantea	+	+	+	+	+	–
Pavona maldivensis	+	–	+	+	+	+
Pavona varians	+	+	+	+	+	+
Pavona chiriquiensis	+	+[8]	+	+	––	–
Pavona cf. *duerdeni*	–	–	–	+-	+	+
Cycloseris curvata	+	+	+	+	–	+
Diaseris distorta	+	+	+	+	+	+
Totals	22	20	22	26	20	21

[1]From Glynn (2003), Hickman (2008).
[2]From Glynn (2003), Reyes-Bonilla (2002).
[3]From Zapata & Vargas-Ángel (2003), Glynn & Ault (2000), Reyes-Bonilla (2002).
[4]From Maté (2003), Glynn & Ault (2000), Guzman et al. (2008), Reyes-Bonilla (2002).
[5]From Glynn & Ault (2000), Glynn (2003).
[6]From Veron (2000).
[7]*P. verrucosa* and *P. elegans* considered conspecific by P. Glynn and counted as one species in the totals.
[8]Needs verification.

during the unsettled Neogene period. An alternative vicariance hypothesis (McCoy & Heck 1976, Heck & McCoy 1978) proposed that the east Pacific coral communities are derived from a widespread pan-Tethyan coral biota that was widely distributed across the Central American seaway. After the Pliocene closure of the seaway *c.* 3.5–3 million years ago, surviving fauna were modified by tectonic events, speciation and extinction. The vicariance hypothesis has been criticized by several authors and rejected by Veron (1995 and references cited) but Glynn & Ault (2000) caution that it seems premature to dismiss the hypothesis at this time. It is also possible that remnants of the extensive Neogene fauna may have survived in the east Pacific following closure of the Central American seaway, to be augmented by dispersal from the west (Glynn & Wellington 1983), a view that favors contributions from both vicariance and long-distance dispersal to the modern east Pacific coral fauna.

There seems little question that long-distance dispersal of pelagic, planktotrophic larvae has contributed to the recovery of equatorial east Pacific reefs destroyed by recent El Niño events. As evidence, Guzman & Cortes (2007) point to the recent appearance at Cocos Island of several coral species that had not been reported before the mid-1990s. The Line Islands are considered the principal source of east Pacific corals by way of the NEC. While this current lies well north of Galapagos (Fig. 1), several lines of evidence attest to the dispersal of coral larvae (and both larvae and adults of other marine taxa) by warm gyres from the NEC to the islands, especially during El Niño activity. "Dispersal pulses" that could provide rapid transport of coral larvae to the Galapagos would be favored during such anomalous conditions (Glynn & Wellington 1983). Glynn & Ault (2000), recognizing that the East Pacific Barrier is more a hindrance to eastward larval dispersal than a complete impediment, suggest that the barrier should more appropriately be termed an east Pacific filter bridge.

The ahermatypic (azooxanthellate) corals of the equatorial east Pacific represent a much richer and more diverse fauna than the hermatypic corals. Approximately 105 species are recognized from the east Pacific and 43 are recorded from the Galapagos (Cairns 1991 and pers. comm.). Unlike the hermatypic corals, none of which is endemic to Galapagos, 17 of the 43 ahermatypic species (39.5%) are peculiar to the Galapagos (Table 1). Twenty-three of the 43 species are deep water. If shallow-water ahermatypes only are considered, the percentage of endemicity drops to 29%. Twenty ahermatypes (47%) have Panamic affinity and 14 (33%) have Indo-Pacific affinity. Six (14%) are cosmopolitan. These percentages contrast markedly with the hermatypic corals, which have 86% Panamic affinity and 86% Indo-Pacific or Central Pacific affinity.

As a distinct faunal group, ahermatypes occur worldwide, exploit a wide range of ecological niches, and are not limited to shallow, sunlit waters as are the hermatypic corals. Many thrive in deep ocean, under rocks, and in ledges and caves where light is absent or minimal. The faunistic affinities of Galapagos ahermatypes resemble those of molluscs with a high endemic component and strong Panamic affinities, followed by Indo-Pacific and cosmopolitan affinities. Because an ahermatypic faunal analysis from Ecuador and Pacific Colombia comparable to that from Galapagos is not yet available, we can only speculate that the ahermatypic composition of Galapagos appears well represented as compared to the mainland.

ECHINODERMS

Echinoderms are well represented in Galapagos with nearly 200 species, although nearly two-thirds of these are deep-water species that do not appear in shallow-water surveys. Surveys (Hickman 1997) and published information (Maluf 1988, 1991) yield a total of 84 species in shallow-water Galapagos. Removing species that have not appeared in recent surveys, single records that may be strays, and suspected mistaken literature reports, the total is reduced to 73 verifiable species. This exceeds the 65 verified species of the Colombian Pacific coast, where both the basic taxonomic work and shallow-water ecosystems parallel those of Galapagos (Table 7). The results of recent surveys from the Ecuadorian coast were not available at this writing. Species shared by Galapagos and Pacific Colombia range from 29% for ophiuroids and echinoids, to 43% for asteroids and 50% for holothuroids. Holothuroids are especially well represented in Galapagos, with 18 shallow-water species compared to 12 in Colombia. The 26 echinoids of Galapagos compare with Colombia's 16 species (Neira & Cantera 2005) and the 33 species found in Panama (Lessios 2005). Of the 33 Panama species, 20 occur in Galapagos, attesting to the strong Panamic affinity of Galapagos echinoderms. Oddly, ten echinoid species shared between Panama and Galapagos have not been recorded from Pacific Colombia.

Approximately 8% of Galapagos shallow-water echinoderms are endemic (one asteroid, three ophiuroids

Table 7. Representation of shallow-water (<30 m) echinoderms of Galapagos, Pacific Colombia and the east Pacific.

Class	Galapagos[1]	Colombia[2]	E Pacific[3]
Asteroidea	20	22	62
Ophiuroidea	13	16	86
Echinoidea	21	16	55
Holothuroidea	18	13	71
Crinoidea	1 (?)	0	1
Totals	**73**	**67**	**275**

[1]From Maluf (1988, 1991), Hickman (1997).
[2]From Neira & Cantera (2005), M. Cohen (pers. comm.).
[3]E Pacific = Central East Pacific of Maluf (1988), *i.e.* between Pt Conception, California and S Peru (34°30′N to *c.* 18°S).

and two echinoids), although collecting has not been as methodical along the Ecuadorian mainland coast as it has in Galapagos. The inclusion of deep-water endemics brings total endemism to 18% (Maluf 1991), a higher percentage than in other east Pacific islands, where it varies from 0% for Clipperton to 9% for Cocos (Maluf 1991). The higher percentage in Galapagos may be an archipelago effect, with greater opportunity for isolation and speciation. However, currents probably distribute larvae throughout the islands, suggesting that there is little opportunity for allopatric speciation within the archipelago. Additionally, sampling effort has been very uneven among the east Pacific islands, suggesting caution in evaluating comparisons of endemism. As with the molluscs, echinoderm endemism is at the species level; there are no endemic echinoderm genera in the Galapagos Islands.

Like the marine molluscs, the Galapagos echinoderms have affinities with neighboring Pacific regions but are dominated by Panamic species. In general echinoderms have been more successful in long-distance colonization than marine molluscs and porcelain crabs. All echinoderm classes except the crinoids are well represented in Galapagos. Of the shallow-water (<200 m) echinoderms, 12% have Indo-Pacific affinities, 8% are cosmopolitan, and 8% are shared with the California province (Maluf 1991).

HYDROIDS AND BRYOZOANS

The preceding examples suggest that for Galapagos, as for other oceanic islands, three agents act as determinants for colonization of marine invertebrates that are dependent primarily upon larval dispersal: habitat substrate, currents and temperature, and isolation. However, these conditions may not be limiting to groups less dependent upon larval dispersal, such as hydroids of the phylum Cnidaria and bryozoans of the phylum Ectoprocta. All marine species within these two groups are colonial.

Although the hydroid fauna along several areas of the mainland east Pacific coastline is poorly known, 125 species have been identified from the Panamic province. Diversity is high in Galapagos, with 96 known species and 14 (14.5%) considered endemic (Calder *et al*. 2003), a relatively high percentage for a group with good dispersal potential. Hydroids are poorly equipped for long-distance dispersal by medusae or larvae. Instead they attach to floating objects, such as logs, debris, and hulls of ships. Long-range dispersal in this manner by the "sessile" benthic stage of the animal is much more successful than by its free-swimming reproductive stage.

Bryozoans are tiny, sessile, colony-building animals that are ubiquitous in the marine environment. Some form erect, branching colonies that resemble seaweed but most form limy encrustations on almost any solid surface. Fig. 6, showing the underside of a rock collected from Cousins islet in 2002, emphasizes the widespread

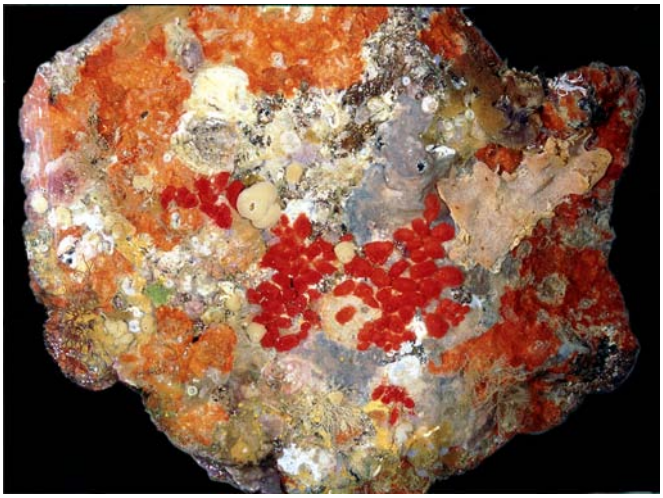

Figure 6. Underside of a rock recovered at Cousins Island, on which were growing 12 species of bryozoans, as well as sponges, ascidians and hydroids.

presence of bryozoans in Galapagos. On this 30 cm rock were 12 species of bryozoans, in addition to numerous ascidians, hydroids, and sponges.

Surveys and collections made before 1990 yielded 184 species of bryozoans in Galapagos (Banta & Redden 1990). This impressive total, which almost certainly is an underestimate, is comparable to the most diverse bryozoan faunas known (Banta 1991). The greatest affinity is with the Panamic province, but with good representation of both northern (California, 85 species) and southern (Peru–Chile, 24 species) provinces (Table 8), while 28% have affinities with the Indo-Pacific, which attests to the effective dispersal of bryozoans. Eighteen percent are endemic, compared with 14–16% for shore fishes (McCosker 1998), 19% for brachyuran crabs (Garth 1991), 14.5% for hydroids, and 19% for molluscs (Finet 1991).

Only two families of bryozoans with six species have planktotrophic larvae, but they are not better represented than those with other larval types. So, as with hydroids, dispersal is mainly by rafting on floating debris or transport on the hulls of ships in the adult stage, as well as by larvae. Adults are planktotrophic, making

Table 8. Zoogeographic affinities of Galapagos bryozoans (184 species) (from Banta 1991).

Affinity	No. of species	%[1]
Panamic	148	80
California	85	46
Peru–Chile	24	13
Endemic	34	18
Indo-Pacific	51	28

[1]Percentages total more than 100 because many species have affinities with more than one province.

survival more likely and increasing the chance of establishment of a permanent population once transport is accomplished.

EVOLUTION OF GALAPAGOS ENDEMICS

Endemism among Galapagos invertebrates occurs by one of two processes. When a species colonizes the islands from a distant source and then becomes extinct outside the archipelago, the Galapagos population represents a biogeographic relict (allochthonous endemic). The alternative is allopatric speciation, when a species colonizes the islands and its population there diverges through drift and/or selection (creating autochthonous endemics). Given the short life of oceanic islands due to erosion and subsidence, we might expect there to be insufficient time for the extinction of all conspecific populations of a species found outside the archipelago, especially in the case of species that were sufficiently abundant elsewhere to have managed to colonize the islands in the first place. Consequently, the allopatric model leading to autochthonous endemics is usually assumed to be the more common of the two processes on oceanic islands. Since the Galapagos islands are separated by deep ocean, repeated rounds of allopatric speciation could occur within the archipelago itself, by infrequent dispersal from island to island. In this case, the result would be a cluster of sister species, all endemic to the archipelago and, at least at first, with endemic congeners on separate islands. Such a pattern is seen in many of the terrestrial animals (*e.g*. mockingbirds *Nesomimus* and tortoises *Geochelone*) and plants (*e.g*. *Scalesia*) of Galapagos.

Terrestrial plant and animal genera found on the Galapagos and other oceanic islands are commonly represented by many endemic sister species. Many genera of vascular plants and several animal groups have undergone such radiations on the islands. In contrast, among the marine invertebrates no genus comprises more than one endemic species. The failure of marine invertebrates to experience archipelago speciation may reflect slower speciation of marine invertebrates, a claim made by paleontologists (*e.g*. James 1984), as well as the greater gene flow between shallow water habitats. The absence of any marine invertebrate genera that are endemic to Galapagos, in contrast to the land fauna, may also reflect these factors.

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